

# Can functional traits explain phylogenetic signal in the composition of a plant community?

Daijiang Li<sup>1\*</sup>, Anthony R. Ives<sup>2</sup>, Donald M. Waller<sup>1</sup>

<sup>1</sup>Department of Botany, University of Wisconsin, 430 Lincoln Drive, Madison, Wisconsin, 53706

<sup>2</sup>Department of Zoology, University of Wisconsin, 430 Lincoln Drive, Madison, Wisconsin, 53706

Emails: [daijianglee@gmail.com](mailto:daijianglee@gmail.com); [arives@wisc.edu](mailto:arives@wisc.edu); [dmwaller@wisc.edu](mailto:dmwaller@wisc.edu)

\* Correspondence: Daijiang Li, Tel: (608) 265-2191

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22 **Abstract:**

23 Phylogeny-based and functional trait-based analyses are used widely to study community  
24 composition. In principle, knowing all information about species traits should completely explain  
25 phylogenetic patterns in community composition. In reality, phylogenies may contain more  
26 information than the collection of measured traits. The extent to which functional trait  
27 information makes phylogenetic information redundant, however, is unknown. We used  
28 phylogenetic linear mixed models to analyze community composition of 55 understory plant  
29 species distributed across 30 forest sites in central Wisconsin. These communities showed strong  
30 phylogenetic attraction. Most of the 15 measured functional traits showed strong phylogenetic  
31 signal, but they only reduced the strength of phylogenetic community patterns in the abundances  
32 and presence/absences of co-occurring species by 57% and 89%, respectively, falling short of  
33 fully explaining phylogenetic community structure. Our study demonstrates the value of  
34 phylogenies in studying of community composition, especially with abundance data, even when  
35 rich functional trait data are available.

36 **Introduction**

37 Functional traits, arising as innovations through evolution, can capture essential aspects of  
38 species' morphology, ecophysiology, and life-history strategy (McGill *et al.* 2006; Violle *et al.*  
39 2007). Although closely related species can differ greatly in some functional traits due to rapid  
40 evolution or ecological convergence (Losos, 2008, 2011), most functional traits show strong  
41 phylogenetic signal (Freckleton *et al.* 2002; Webb *et al.* 2002, Moles *et al.* 2005, Donoghue  
42 2008). Functional traits, with or without phylogenetic signal, are known to influence the species  
43 composition of communities, thereby providing mechanistic links between fundamental

44 ecological processes and community structure (McGill *et al.* 2006; Violle *et al.* 2007; Adler *et al.*  
45 2013). Functional traits also provide a common currency that facilitates comparisons among  
46 species and across regions, allowing us to assess the generality of patterns and predictions in  
47 community ecology (McGill *et al.* 2006). This has led to a proliferation of studies using  
48 functional traits to understand community composition. Functional trait-based approaches,  
49 however, are limited by the fact that it is impossible to measure all potentially important  
50 functional traits affecting the distribution of species.

51 Even in the absence of functional trait information, it is still possible to infer the effects of  
52 (unmeasured) functional traits on community composition by investigating phylogenetic patterns  
53 in community composition. Phylogenies play an important role in community ecology by giving  
54 information about evolutionary relationships among species (Graves & Gotelli, 1993; Losos  
55 1996; Baum & Smith, 2012). Because phylogenetically related species often share similar  
56 functional trait values, we expect phylogenetically related species to co-occur more often in the  
57 same communities reflecting their shared environmental tolerances. Conversely, if  
58 phylogenetically related species have similar traits that cause them to compete with each other,  
59 then closely related species may be less likely to co-occur. These and other processes relating  
60 functional traits to community composition likely lead to phylogenetic signatures in how species  
61 are distributed among communities (Webb *et al.* 2002). However, in principle, if we have  
62 information for all relevant functional traits, then we expect phylogeny to provide little  
63 additional information relevant for community composition. That is, when all of the functional  
64 traits affecting community composition are known, we do not expect the unexplained residual  
65 variation in the occurrence of species to have phylogenetic signal (Ives & Helmus, 2011).

66 In practice, we cannot obtain information about all relevant functional traits. In addition,  
67 phylogenetic signals in community composition may result from factors beyond functional traits,  
68 such as the biogeographical patterns generated as species disperse across a landscape (Ricklefs *et*  
69 *al.* 1993; Moen *et al.* 2009). If these forces are important, then even after accounting for all  
70 functional traits whose measurements are available, we should expect phylogenies to contain  
71 additional information about community composition (Vane-Wright *et al.* 1991; Cadotte *et al.*  
72 2009). Thus far, however, we are aware of no study that has explicitly assessed the overlap  
73 between information from traits versus phylogeny. Here, we ask how much of the phylogenetic  
74 signal in the composition of a plant community assemblage can be explained by functional traits  
75 (Fig. 1).

76 We analyzed data on the abundance of 55 understory plant species distributed across 30  
77 Wisconsin pine barrens sites (Li & Waller 2015). For each species, we had data on 15 functional  
78 traits and a recent highly resolved phylogeny (Cameron *et al. unpublished manuscript*<sup>1</sup>). At each  
79 site, we measured 20 environmental variables. Below, we first investigate whether there is  
80 phylogenetic pattern in community composition, using a phylogenetic community mixed model  
81 that tests for both “phylogenetic attraction” (phylogenetically related species more likely to occur  
82 in the same communities) and “phylogenetic repulsion.” If there is phylogenetic pattern, then it  
83 could be produced by measured functional traits that themselves have phylogenetic signal (Fig.  
84 1, arrows 2, 4, and 7), unmeasured functional traits with phylogenetic signal (Fig. 1, arrows 2, 5,  
85 and 8), or phylogenetic processes unrelated to functional traits (Fig. 1, arrow 6). We then  
86 developed a phylogenetic community mixed model incorporating the measured functional traits  
87 to ask whether there is phylogenetic signal in the residual variation in community composition

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<sup>1</sup> Cameron, K., R. Kriebel, M. Pace, D. Spalink, P. Li, and K. Sytsma. *In prep.* A complete molecular community phylogeny for the flora of Wisconsin based on the universal plant DNA barcode.

88 after the effects of these traits are removed. This analysis tests the hypothesis that we can explain  
89 all of the phylogenetic pattern in community composition using measured functional traits.  
90 Finally, we use a phylogenetic community mixed model to investigate whether phylogenetically  
91 related species respond similarly to environmental gradients across the communities. The  
92 motivation for this final analysis is to indirectly identify possible unmeasured functional traits  
93 that might play a role in community assembly. In cases where phylogenetically related species  
94 respond similarly to an environmental gradient, species presumably share traits that confer  
95 similar tolerances to, or preferences for, specific environmental conditions. Thus, this final  
96 analysis could point towards additional functional traits that might be relevant for explaining  
97 patterns in community composition.

98

## 99 **Methods**

### 100 **Data**

101 *Community composition.* – We sampled 30 pine barrens forest sites in the central Wisconsin sand  
102 plains in 2012 using 50 1- $m^2$  quadrats placed along five transects at each site. Within each  
103 quadrat, we recorded the presence/absence of all understory vascular plant species (see Li &  
104 Waller 2015 for details). Across all sites, we recorded 152 species. For the analyses other than  
105 the initial exploration of phylogenetic patterns in community composition, we focused on the 55  
106 species that occurred in three or more communities. We did this because we did not have  
107 functional trait data for many rare species, and we also wanted to limit the number of zeros in the  
108 data set.

109 *Functional traits.* – For the 55 focal species, we measured 11 continuous and four categorical  
110 functional traits on at least 12 individuals (four from each of at least three populations) using  
111 standard protocols (Pérez-Harguindeguy *et al.* 2013). Continuous traits include seed mass  
112 (g/seed), plant height (cm), specific leaf area (SLA,  $m^2/kg$ ), leaf dry matter content (LDMC, %),  
113 leaf circularity (dimensionless), leaf length (cm), leaf width (cm), leaf thickness (mm), leaf  
114 carbon concentration (%), leaf nitrogen concentration (%), and stem dry matter content (SDMC,  
115 %). We aggregated categories of each categorical trait into two levels: growth form (woody vs.  
116 non-woody), life cycle (annual vs. non-annual), and pollination mode (biotic vs. abiotic). We  
117 divided seed dispersal mode into three binary variables (wind dispersed vs. not, animal dispersed  
118 vs. not, and unassisted vs. assisted dispersal). Collectively, these functional traits, covering the  
119 leaf-height-seed (LHS) plant ecology strategy (Westoby, 1998), represent multidimensional  
120 functions of plants associated with resource use, competitive ability, dispersal ability, etc. For  
121 analyses, we log-transformed highly skewed traits first and then Z-transformed the trait values to  
122 have means of zero and standard deviations of one, allowing coefficients in the mixed models to  
123 be interpreted as effect sizes.

124 *Phylogeny.* – The phylogeny used in this study is a subset of a phylogeny for all vascular plants  
125 in Wisconsin (Cameron *et al. unpublished manuscript*). Briefly, Cameron *et al.* used two plastid  
126 DNA barcode loci *rbcL* and *matK* to build the phylogeny using maximum likelihood (ML) in the  
127 program R<sub>AXML</sub> (Stamatakis, 2014). The phylogeny was then time-calibrated using the branch  
128 length adjuster (*bladj*) available in the program *phylocom* (Webb *et al.* 2008).

129 *Environmental data.* – At each site, we pooled six soil samples to measure the soil properties  
130 listed in Table 4. We also took six vertical fish-eye photographic images at each site to measure  
131 canopy cover. To characterize climatic conditions, we extracted daily precipitation and minimum

132 temperature for each site from interpolated values estimated by Kucharik *et al.* (2010) from 2002  
133 to 2006 (data after 2006 were not available). All environmental variables were Z-transformed.

## 134 **Phylogenetic community composition**

135 We performed all analyses using both species abundances and species presence/absences among  
136 communities. In the main text we present the analyses of abundance data, because including  
137 abundance data in phylogenetic community analyses provides more information about  
138 community assembly (Freilich & Connolly, 2015). In the Appendix we present the results for  
139 presence/absence data.

140 We first tested for phylogenetic community structure without including environmental or  
141 functional trait information. We used traditional metrics and randomization tests (i.e., null  
142 models) to identify whether there was phylogenetic pattern (phylogenetic attraction or repulsion)  
143 in the composition of our 30 communities. Specifically, we measured the phylogenetic structure  
144 of species abundances at each site using phylogenetic species evenness (PSE, Helmus *et al.*  
145 2007) and mean phylogenetic distance (MPD, Webb, 2000). For each site, we calculated PSE  
146 and MPD, and then calculated the mean of these metrics ( $\overline{\text{PSE}}_{\text{obs}}$  and  $\overline{\text{MPD}}_{\text{obs}}$ ) across all 30  
147 sites. To test for phylogenetic pattern, we permuted species randomly among sites (SIM2 in  
148 Gotelli, 2000) 4999 times and then calculated metrics base on each permutation data set. If  
149  $\overline{\text{PSE}}_{\text{obs}}$  or  $\overline{\text{MPD}}_{\text{obs}}$  falls below (or above) 97.5% of the permutation values, then we infer a  
150 statistically significant phylogenetic attraction (or repulsion). This null permutation model  
151 retains the prevalence of each species across sites, but allows sites to change in species richness.  
152 Using this null model where sites can vary in species richness is justified, because under the null  
153 hypothesis of no phylogenetic signal, the values of PSE and MPD are independent of species

154 richness at the sites. We also performed permutation tests on the presence/absence of species  
155 from the 30 sites using phylogenetic species variation (PSV, Helmus *et al.* 2007) and MPD.  
156 In addition to these permutation tests, we fit a phylogenetic linear mixed model (PLMM) to test  
157 for phylogenetic community patterns in species abundances. A PLMM establishes a flexible  
158 statistical base to subsequently incorporate functional trait and environmental variables.  
159 Furthermore, PLMMs tend to have greater statistical power than permutation tests (Ives &  
160 Helmus, 2011). To build the PLMM, let  $n$  be the number of species distributed among  $m$  sites.  
161 Letting  $Y$  be the  $mn \times 1$  vector containing the abundance of species  $j$  ( $j = 1, \dots, n$ ) at site  $s$  ( $s = 1,$   
162  $\dots, m$ ), the PLMM is

$$\begin{aligned} 163 \quad \log(Y + 1) &= \alpha + a_{\text{spp}[i]} + b_{\text{spp}[i]} + c_i + d_{\text{site}[i]} + e_i \\ 164 \quad a &\sim \text{Gaussian}(\mathbf{0}, \sigma_a^2 \mathbf{I}_n) \\ 165 \quad b &\sim \text{Gaussian}(\mathbf{0}, \sigma_b^2 \Sigma_{\text{spp}}) \\ 166 \quad c &\sim \text{Gaussian}(\mathbf{0}, \text{kron}(\mathbf{I}_m, \sigma_c^2 \Sigma_{\text{nested}})) \\ 167 \quad d &\sim \text{Gaussian}(\mathbf{0}, \sigma_d^2 \mathbf{I}_m) \\ 168 \quad e &\sim \text{Gaussian}(\mathbf{0}, \sigma_e^2 \mathbf{I}_{mn}) \end{aligned} \tag{1}$$

169 We use the convention of multilevel models here (Gelman & Hill, 2007), with fixed and random  
170 effects given by Greek and Latin letters, respectively. The function  $\text{spp}[i]$  maps the observation  $i$   
171 in vector  $Y$  to the identity of the species (Gelman & Hill, 2007, p251-252), so  $i$  takes values from  
172 1 to  $mn$ . The intercept  $\alpha$  estimates the overall average log abundance of species across all sites.  
173 The following three random variables  $a_{\text{spp}[i]}$ ,  $b_{\text{spp}[i]}$  and  $c_i$  incorporate variation in abundance

174 among plant species. Specifically, the  $n$  values of  $a_{\text{spp}[i]}$  give differences among species in mean  
175 log abundance across all sites and are assumed to be drawn independently from a Gaussian  
176 distribution with mean 0 and variance  $\sigma_a^2$ . The  $n$  values of  $b_{\text{spp}[i]}$  also give differences in mean log  
177 abundance across sites but are assumed to be drawn from a multivariate Gaussian distribution  
178 with covariance matrix  $\sigma_b^2 \Sigma_{\text{spp}}$ , where the  $n \times n$  matrix  $\Sigma_{\text{spp}}$  is derived from the phylogeny (see  
179 next paragraph), and the scalar  $\sigma_b^2$  dictates the overall strength of the phylogenetic signal. Thus,  
180  $a_{\text{spp}[i]}$  and  $b_{\text{spp}[i]}$  together capture variation in mean species log abundances that is either unrelated  
181 to phylogeny or has phylogenetic signal. The random variable  $c_i$  accounts for covariance in the  
182 log abundances of plant species nested within sites (using the Kronecker product,  $\text{kron}$ ).  
183 Specifically,  $c_i$  assesses whether phylogenetically related plant species are more or less likely to  
184 co-occur at the same sites. Hence,  $c_i$  is used to measure either phylogenetic attraction or  
185 phylogenetic repulsion; because  $\sigma_c^2$  dictates the overall strength of these phylogenetic patterns, it  
186 is the key term we are interested in. Random effect  $d_{\text{site}[i]}$  is assumed to contain  $m$  values, one for  
187 each site, that are distributed by a Gaussian distribution with variance  $\sigma_d^2$  to account for  
188 differences in the average log abundances of species from site to site. Finally,  $e_i$  captures residual  
189 variance  $\sigma_e^2$ .

190 We derived the phylogenetic covariance matrix  $\Sigma_{\text{spp}}$  from the assumption of Brownian motion  
191 evolution. If a continuous-valued trait evolves up a phylogenetic tree with a constant probability  
192 of slight increases or decreases, the covariance in trait values between two species will be  
193 proportional to the length of shared evolution, given by the distance on the phylogenetic tree  
194 between the root and the species' most recent common ancestor (Martins & Hanson 1997). This  
195 gives a direct way to convert the phylogeny into a hypothesis about the covariance matrix. For  
196 the assessment of phylogenetic attraction within sites,  $c_i$ , we use  $\Sigma_{\text{nested}} = \Sigma_{\text{spp}}$ . For phylogenetic

197 repulsion, we use the matrix inverse of  $\Sigma_{\text{spp}}$ ,  $\Sigma_{\text{nested}} = (\Sigma_{\text{spp}})^{-1}$ . Theoretical justification for  $\Sigma_{\text{nested}}$   
198  $= (\Sigma_{\text{spp}})^{-1}$  comes from a model of competition among community members (Ives & Helmus  
199 2011, Appendix A). Briefly, if the strength of competition between species is given by  $\Sigma_{\text{spp}}$ , as  
200 might be the case if closely related species are more likely to share common resources, then the  
201 relative abundances of species will have covariance matrix  $(\Sigma_{\text{spp}})^{-1}$ .

202 Equation 1 is the same as model I in Ives & Helmus (2011), except model I includes variation  
203 among species in mean log abundance across sites as fixed effects rather than two random  
204 effects,  $a_{\text{spp}[i]}$  and  $b_{\text{spp}[i]}$ . This change allows us to align equation 1 with equation 3 (below) that  
205 includes variation in the relationship between trait values and log abundance within sites as  
206 random effects. In our analyses, treating variation among species in mean log abundance as fixed  
207 effects (results not presented) led to almost identical estimates of phylogenetic signal (estimates  
208 of  $\sigma_c^2$ ), and therefore our treatment of  $a_{\text{spp}[i]}$  and  $b_{\text{spp}[i]}$  as random effects does not change the  
209 conclusions.

210 We fit the PLMM with maximum likelihood using function `communityPGLMM` in the `pez`  
211 (Pearse *et al.*, 2015) package of R (R Core Team, 2015). Statistical significance of the variance  
212 estimates  $\sigma^2$  was determined using a likelihood ratio test. Because the null hypothesis  $\sigma^2 = 0$  is on  
213 the boundary of the parameter space ( $\sigma^2$  cannot be negative), we used the  $0.5\chi_0^2 + 0.5\chi_1^2$  mixture  
214 distribution of Self & Liang (1987) for significance tests. The distribution of  $\chi_0^2$  represents a  
215 distribution with a point mass at 0, and the  $p$ -values given by the constrained likelihood ratio test  
216 are one-half the values that would be calculated from a standard likelihood ratio test using  $\chi_1^2$ .  
217 Simulations suggest that  $p$ -values calculated in this way are more conservative (have higher  
218 values) than those from a parametric bootstrap (Appendix Text S1).

219 Our data set contained many zeros (Fig. 2), raising the question of the validity of applying a  
220 linear model to transformed data. Nonetheless, transforming data and applying a linear analysis  
221 is robust when assessing the significance of regression parameters (Ives, 2015).

## 222 **Can functional traits explain phylogenetic community composition?**

223 To quantify how much of the variation in phylogenetic patterns can be explained by measured  
224 functional traits, we estimated PLMMs with and without functional traits, and then compared the  
225 strength of phylogenetic signal in the residual variation: if functional traits alone serve to explain  
226 phylogenetic community composition, then as functional traits are included, the strength of the  
227 phylogenetic signal in the residuals should decrease. We selected functional traits one by one  
228 based on the two conditions necessary for them to generate phylogenetic signal in community  
229 composition. First, a functional trait must show phylogenetic signal among species, because in  
230 the absence of phylogenetic signal among species, a trait could not produce phylogenetic signal  
231 in species' abundances. Second, there must be variation among sites in the relationship between  
232 species trait values and abundances; if a trait has phylogenetic signal but there is no variation in  
233 relationships between plant functional trait values and abundances among sites, then it will  
234 contribute to the overall phylogenetic signal of species abundance and will be captured by  $b_{\text{spp}[i]}$   
235 in equation 1, but it will not affect phylogenetic co-occurrence patterns captured by  $c_i$ . Therefore,  
236 we only investigate traits that exhibit both strong phylogenetic signal and variation among sites  
237 in the apparent advantages the traits give to species.

238 We tested the phylogenetic signal for each functional trait using model-based methods. Each  
239 continuous trait was tested with Pagel's  $\lambda$  (Pagel, 1999) using `phy1o1m` (Ho & Ané, 2014). For  
240 the binary traits, we applied phylogenetic logistic regression (Ives & Garland, 2010) as

241 implemented by `phyloglm` (Ho & Ané, 2014). We also tested phylogenetic signal of functional  
 242 traits via Blomberg's  $K$  (Blomberg *et al.* 2003) with `picante` (Kembel *et al.* 2010).

243 We tested variation of relationships between trait values and log abundances with the LMM

$$244 \quad \log(Y + 1) = \alpha + a_{\text{spp}[i]} + (\beta + b_{\text{site}[i]})t_{\text{spp}[i]} + e_i$$

$$245 \quad a \sim \text{Gaussian}(\mathbf{0}, \sigma_a^2 \mathbf{I}_n)$$

$$246 \quad b \sim \text{Gaussian}(\mathbf{0}, \sigma_b^2 \mathbf{I}_m)$$

$$247 \quad e \sim \text{Gaussian}(\mathbf{0}, \sigma_e^2 \mathbf{I}_{mn}) \quad (2)$$

248 where  $t_{\text{spp}[i]}$  is the focal functional trait value of the species corresponding to observation  $i$ , and  $\sigma_b^2$   
 249 gives the variation among sites in the relationship between species trait values and log  
 250 abundances. This formulation is closely related to the model used by Pollock *et al.* (2012). If  $\sigma_b^2$   
 251  $> 0$ , we conclude that different sites select species differently based on the tested trait. We use  $p$   
 252  $< 0.1$  here to lower the risk of excluding potential important functional traits.

253 We quantified the contribution of a trait to the observed phylogenetic pattern in community  
 254 composition using the model

$$255 \quad \log(Y + 1) = \alpha + a_{\text{spp}[i]} + b_{\text{spp}[i]} + c_i + d_{\text{site}[i]} + (\beta + f_{\text{site}[i]})t_{\text{spp}[i]} + e_i$$

$$256 \quad a \sim \text{Gaussian}(\mathbf{0}, \sigma_a^2 \mathbf{I}_n)$$

$$257 \quad b \sim \text{Gaussian}(\mathbf{0}, \sigma_b^2 \Sigma_{\text{spp}})$$

$$258 \quad c \sim \text{Gaussian}(\mathbf{0}, \text{kron}(\mathbf{I}_m, \sigma_c^2 \Sigma_{\text{nested}}))$$

$$259 \quad d \sim \text{Gaussian}(\mathbf{0}, \sigma_d^2 \mathbf{I}_m)$$

$$\begin{aligned} 260 \quad f &\sim \text{Gaussian}(\mathbf{0}, \sigma_f^2 \mathbf{I}_m) \\ 261 \quad e &\sim \text{Gaussian}(\mathbf{0}, \sigma_e^2 \mathbf{I}_{mn}) \end{aligned} \quad (3)$$

262 This model is the same as equation 1 used to assess phylogenetic patterns in community  
263 composition, except that it includes functional trait values  $t_{\text{spp}[i]}$ . The proportion of phylogenetic  
264 signal in species composition (estimated by  $\sigma_c^2$ ) that trait  $t_{\text{spp}[i]}$  can explain is assessed by  
265 comparing  $\sigma_c^2$  between models with and without this trait as a product with the random effect  
266  $f_{\text{site}[i]}$ . Finally, to evaluate the overall contribution of functional traits to the observed  
267 phylogenetic patterns, we built a multivariate version of equation 3 which included all traits that  
268 have both phylogenetic signal and strong variation among sites.

### 269 **Does any environmental variable drive phylogenetic pattern?**

270 If phylogenetic patterns in community composition are observed, yet no functional traits can  
271 explain the patterns, how could we identify additional functional traits that might be responsible?  
272 Phylogenetically related species usually are assumed to be ecologically similar due to niche  
273 conservatism (Wiens *et al.* 2010). Therefore, related species will tend to have similar responses  
274 to environmental variables. If these environmental variables are strong enough to drive  
275 phylogenetic patterns in community composition, then functional traits that are associated with  
276 tolerance or sensitivity to these environmental variables will likely be important in explaining  
277 community composition. Thus, we investigated phylogenetic patterns in the responses of species  
278 to environmental variables to suggest additional, unmeasured functional traits that might be  
279 important to explain phylogenetic patterns in community composition.

280 We tested for phylogenetic patterns in the responses of species to environmental variables using  
281 the PLMM

$$282 \quad \log(Y + 1) = \alpha + a_{\text{spp}[i]} + b_{\text{spp}[i]} + (\beta + g_{\text{spp}[i]} + h_{\text{spp}[i]})x_{\text{site}[i]} + e_i$$

$$283 \quad a \sim \text{Gaussian}(\mathbf{0}, \sigma_a^2 \mathbf{I}_n)$$

$$284 \quad b \sim \text{Gaussian}(\mathbf{0}, \sigma_b^2 \Sigma_{\text{spp}})$$

$$285 \quad g \sim \text{Gaussian}(\mathbf{0}, \sigma_g^2 \mathbf{I}_n)$$

$$286 \quad h \sim \text{Gaussian}(\mathbf{0}, \sigma_h^2 \Sigma_{\text{spp}})$$

$$287 \quad e \sim \text{Gaussian}(\mathbf{0}, \sigma_e^2 \mathbf{I}_{mn}) \quad (4)$$

288 Here,  $g_{\text{spp}[i]}$  and  $h_{\text{spp}[i]}$  represent non-phylogenetic and phylogenetic variation among species in  
289 their response to environmental variable  $x$  (see model II in Ives & Helmus, 2011). The key  
290 parameter of interest is  $\sigma_h^2$ , which we tested using a likelihood ratio test. If  $\sigma_h^2 > 0$ ,  
291 phylogenetically related species respond to environmental variable  $x$  in similar ways, suggesting  
292 the existence of an unmeasured phylogenetically inherited trait that is associated with species  
293 tolerances or sensitivities to  $x$ . Given the large number of environmental variables in our data set,  
294 we first applied equation 4 without the term  $b_{\text{spp}[i]}$  and  $h_{\text{spp}[i]}$ , and selected environmental  
295 variables for which there was variation in responses among species given by  $g_{\text{spp}[i]}$  regardless of  
296 whether this variation was phylogenetic. For variables  $x$  for which  $\sigma_g^2 > 0$  in the reduced version  
297 of equation 4, we then applied the full equation 4 and tested whether  $\sigma_h^2 > 0$ .

298

## 299 Results

### 300 Phylogenetic community composition

301 Phylogenetically related species co-occurred more often than expected by chance in pine barrens  
302 communities in central Wisconsin (Fig. 2). Permutation tests including all 152 species showed  
303 that closely related species are likely to have positive covariances in abundance among  
304 communities, as judged by either phylogenetic species evenness ( $\overline{\text{PSE}}_{\text{obs}} = 0.32, p = 0.03$ ) or  
305 mean phylogenetic distance ( $\overline{\text{MPD}}_{\text{obs}} = 338, p = 0.01$ ). In contrast, when we confine analyses to  
306 the 55 focal species that occurring in at least three communities, the permutation tests failed to  
307 show statistically significant phylogenetic patterns (abundance data:  $\overline{\text{PSE}}_{\text{obs}} = 0.27, p = 0.29$ ;  
308  $\overline{\text{MPD}}_{\text{obs}} = 286, p = 0.17$ ; presence/absence data:  $\overline{\text{PSE}}_{\text{obs}} = 0.31, p = 0.20$ ;  $\overline{\text{MPD}}_{\text{obs}} = 342, p =$   
309  $0.20$ ). Nevertheless, the PLMM ( $p = 0.008$ ; Table 1) and PGLMM ( $p < 0.001$ ; Appendix Table  
310 S1) both reveal statistically significant phylogenetic patterns for the 55 focal species.

### 311 Can functional traits explain phylogenetic community composition?

312 Most functional traits showed strong phylogenetic signal (Table 2). Five traits – leaf width, leaf  
313 thickness, SLA, leaf circularity, and animal dispersal (marginally significant) – also significantly  
314 affected plant species' abundances among sites ( $\sigma_b^2 > 0$ , equation 2, Table 2), indicating that  
315 different sites selected different species based on these three functional traits. Individually, the  
316 five traits reduced the phylogenetic variance in community composition (as measured by  
317 reduction in  $\sigma_c^2$  in equation 3 when including these traits) by 18%, 8%, 7%, 2%, and 1%,  
318 respectively. Traits that did not pass our two-steps selection individually explained negligible  
319 amount of the phylogenetic variance (all  $< 1\%$  and mostly  $\sim 0\%$ , data not shown), verifying our

320 initial selection of traits. Including all five traits in the final model reduces the phylogenetic  
321 variation  $\sigma_c^2$  by 57%. Thus, the many functional traits we measured in this study can only reduce  
322 the phylogenetic signal in community composition by 57%. Converting the data to  
323 presence/absence and using the PGLMM equivalent of equation 3 reduces  $\sigma_c^2$  by 89% (Appendix,  
324 Table S3). Thus, functional traits explained more of the phylogenetic patterns in the  
325 presence/absence of species from communities than in their log abundance, although functional  
326 traits still cannot fully explain the phylogenetic pattern in community composition.

### 327 **Does any environmental variable drive phylogenetic pattern?**

328 There was significant variation among species in their responses to most of the environmental  
329 variables we measured, including soil conditions, canopy shade, precipitation, and minimum  
330 temperature (Table 4). However, there was no phylogeny signal in the differences among species  
331 in their responses to these variables (last column in Table 4). Therefore, no environmental  
332 variables we measured can explain the observed phylogenetic pattern in community composition.  
333 Using the PGLMM with the presence/absence data, species' responses to minimum temperature  
334 and soil pH, Ca, and Mn concentration all show phylogenetic signal. That is, related species tend  
335 to occupy similar sites as measured by these environmental variables (Appendix Table S4).  
336 Therefore, functional traits associated with these environmental variables could potentially be  
337 responsible for phylogenetic patterns in presence/absence of species among communities.

## 338 **Discussion**

339 We used our extensive database of functional traits to answer a key question in trait-based and  
340 phylogeny-based community ecology: Can information about functional traits explain

341 phylogenetic patterns in community composition? Phylogenetically related plant species are  
342 more likely to reach similar abundances in the same pine barren communities of central  
343 Wisconsin, yet we could not explain this pattern completely using information about species'  
344 functional traits. When functional traits that themselves showed phylogenetic signal among  
345 species were included in the phylogenetic linear mixed model (PLMM) for log abundances of  
346 species in communities, that component of the residual variance having phylogenetic covariances  
347 decreased by only 57%. The decrease in the phylogenetic component of residual variation was  
348 89% in the analyses of presence/absence data, yet even this leaves residual phylogenetic pattern  
349 in the unexplained variation in the presence/absence of species among communities. Thus, even  
350 though we measured 15 functional traits, including most of the standard functional traits used to  
351 analyze plant community structure, we could not fully explain the phylogenetic patterns in  
352 community composition. This suggests that there are either important functional traits that we  
353 have not measured, or that there are phylogenetic processes unrelated to functional traits that we  
354 have not identified. In either case, these results suggest that including phylogenetic information  
355 in addition to functional traits provides further insights into the processes affecting community  
356 assembly.

357 When using the subset of 55 species that occurred in three or more communities, the PLMM  
358 (and PGLMM), but not permutation tests, found statistically significant phylogenetic patterns.  
359 Ives & Helmus (2011) showed that phylogenetic mixed models have greater statistical power  
360 than the metrics like PSE and MPD used with permutation tests. Simulations (Appendix Text S1)  
361 show that PLMM analyses tended to have, if anything, incorrectly low Type I error rates,  
362 implying that our PLMM results were not the result of false positives. We can thus conclude that

363 closely related species are more likely to co-occur and share similar abundances than expected  
364 by chance in these pine barren communities.

365 Incorporating functional traits reduced the phylogenetic component of residual variation in  
366 species composition, what could explain the remaining phylogenetic component? Some  
367 unknown historical process might account for this residual phylogenetic variation (Fig. 1B, IV).  
368 However, our sites are all located within 100 km with each other, making it unlikely that  
369 historical biogeographical processes strongly affect the composition of these communities. It  
370 seems more likely that the main source of phylogenetic patterns that were not explained by our  
371 measured functional traits is additional unmeasured functional traits. Further analyses of the  
372 presence/absence data using PGLMMs suggested that soil conditions (pH, Ca, and Mn levels)  
373 and climate (minimum temperature) are potential driving variables for the residual phylogenetic  
374 patterns (Appendix Table S3). Traits associated with plant responses to these gradients in  
375 environmental conditions could thus account for more of the residual phylogenetic patterns. The  
376 functional traits we measured, however, are traits that are unlikely to capture species-specific  
377 responses to soil and climatic conditions, and we do not have information on likely traits such as  
378 root structure, micorrhizal associations, frost tolerance, etc. We expect such traits might be able  
379 to explain more of the phylogenetic pattern in community composition.

380 We found that functional traits could explain a greater part of the phylogenetic component of the  
381 pattern of species presence/absence (89%) than of species abundances (57%). This is unlikely to  
382 be a statistical artifact. Because we used only the most common 55 species, detection of species  
383 in sites where they occur is likely to be high. In contrast, we expect considerable within-species  
384 variation in our estimates of abundance. Because within-species variation will decrease  
385 phylogenetic signal (Ives *et al.* 2007), we would expect less residual phylogenetic variation in

386 the abundance data than in the presence/absence data, the opposite of what we found. Therefore,  
387 our results suggest that the functional traits we measured have a greater effect on the overall  
388 suitability of sites for species than the finer-tuned quality of the sites to support large  
389 populations, supporting the argument that including abundance data in phylogenetic community  
390 analyses provides more information about community assembly (Freilich & Connolly, 2015).

## 391 **Implications**

392 Our results have several implications for community ecology. First, it is clear that studying  
393 community composition should incorporate analyses of both phylogenetic structure and  
394 functional traits. Phylogenetic and trait information clearly complement each other in allowing  
395 sophisticated analyses that can partition the amount of phylogenetic signal in community  
396 composition that is associated with functional trait variation (Fig. 1). Our results provide  
397 empirical support from community ecology for the argument that phylogenies can provide more  
398 information than a set of discretely measured traits (Vane-Wright *et al.* 1991; Cadotte *et al.*  
399 2009). Although functional traits are necessary to accurately infer the processes driving  
400 phylogenetic patterns (Kraft *et al.* 2007; Cavender-Bares *et al.* 2009), functional traits alone may  
401 often fail to provide a complete picture of community structure.

402 Second, model-based methods are being increasingly applied in ecology because they are more  
403 interpretable, flexible, and powerful than either null models or conventional algorithmic  
404 multivariate analyses (Warton *et al.* 2014). With phylogenetic linear mixed models (PLMM), we  
405 not only detected phylogenetic patterns in community composition, but also assessed the extent  
406 to which these could be explained by functional traits. The ability to combine both phylogenies  
407 and functional traits into the same statistical model using PLMMs (and PGLMMs) provides an

408 integrated and quantitative framework for analyzing ecological communities and predicting  
409 abundance of one taxon from others.

410 Finally, we can use phylogenetic analyses to suggest possible unmeasured functional traits that  
411 underlie patterns in community composition and that therefore should be measured. If species  
412 respond differently to an environmental variable, and if these differences are phylogenetic (i.e.,  
413 related species respond to the environmental variable in similar ways), then there is likely to be a  
414 functional trait or traits that underlie the response of species to this environmental variable. In  
415 our study, the phylogenetic patterns in species responses to edaphic conditions like soil  
416 chemistry highlighted our lack of data on the specific functional traits related to roots or  
417 water/nutrient uptake. While this reveals that our study is incomplete, it also provides a valuable  
418 lesson and demonstrates the power of the integrated PLMM approach.

419

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## 424 **References:**

425 Adler, P.B., Fajardo, A., Kleinhesselink, A.R. & Kraft, N.J.B. (2013). Trait-based tests of  
426 coexistence mechanisms. *Ecol. Lett.*, 16, 1294–1306.

427 Baum, D.A. & Smith, S.D. (2012). *Tree Thinking: An Introduction to Phylogenetic Biology*. 1st  
428 Edition. Roberts Company Publishers, Greenwood Village, Colo.

- 429 Blomberg, S.P., Garland, T. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative  
430 data: Behavioral traits are more labile. *Evolution*, 57, 717–745.
- 431 Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009). Using Phylogenetic,  
432 Functional and Trait Diversity to Understand Patterns of Plant Community Productivity. *PLoS*  
433 *ONE*, 4, e5695.
- 434 Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009). The merging of  
435 community ecology and phylogenetic biology. *Ecol. Lett.*, 12, 693–715.
- 436 Donoghue, M.J. (2008). A phylogenetic perspective on the distribution of plant diversity. *Proc.*  
437 *Natl. Acad. Sci. U.S.A.*, 105, 11549–11555.
- 438 Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002). Phylogenetic Analysis and Comparative  
439 Data: A Test and Review of Evidence. *Am. Nat.*, 160, 712–726.
- 440 Freilich, M.A. & Connolly, S.R. (2015). Phylogenetic community structure when competition  
441 and environmental filtering determine abundances. *Global Ecol. Biogeogr.*, 24, 1390–1400.
- 442 Gelman, A. & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*.  
443 Cambridge University Press.
- 444 Gotelli, N.J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, 81, 2606–  
445 2621.
- 446 Graves, G.R. & Gotelli, N.J. (1993). Assembly of avian mixed-species flocks in Amazonia.  
447 *Proc. Natl. Acad. Sci. U.S.A.*, 90, 1388–1391.
- 448 Helmus, M.R., Bland, T.J., Williams, C.K. & Ives, A.R. (2007). Phylogenetic Measures of  
449 Biodiversity. *Am. Nat.*, 169, E68–E83.
- 450 Ho, L.S.T. & Ané, C. (2014). A linear-time algorithm for Gaussian and non-Gaussian trait  
451 evolution models. *Syst. Biol.*, syu005.
- 452 Ives, A.R. (2015). For testing the significance of regression coefficients, go ahead and log-  
453 transform count data. *Methods Ecol. Evol.*, 6, 828–835.
- 454 Ives, A.R. & Garland, T. (2010). Phylogenetic Logistic Regression for Binary Dependent  
455 Variables. *Syst. Biol.*, 59, 9–26.
- 456 Ives, A.R. & Helmus, M.R. (2011). Generalized linear mixed models for phylogenetic analyses  
457 of community structure. *Ecol. Monogr.*, 81, 511–525.
- 458 Ives, A.R., Midford, P.E. & Garland, T. (2007). Within-Species Variation and Measurement  
459 Error in Phylogenetic Comparative Methods. *Syst. Biol.*, 56, 252–270.

- 460 Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H. & Ackerly, D.D. *et al.*  
461 (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.
- 462 Kraft, N.J.B., Cornwell, W.K., Webb, C.O. & Ackerly, D.D. (2007). Trait Evolution,  
463 Community Assembly, and the Phylogenetic Structure of Ecological Communities. *Am. Nat.*,  
464 170, 271–283.
- 465 Kucharik, C.J., Serbin, S.P., Vavrus, S., Hopkins, E.J. & Motew, M.M. (2010). Patterns of  
466 Climate Change Across Wisconsin From 1950 to 2006. *Phys. Geogr.*, 31, 1–28.
- 467 Li, D. & Waller, D. (2015). Drivers of observed biotic homogenization in pine barrens of central  
468 Wisconsin. *Ecology*, 96, 1030–1041.
- 469 Losos, J.B. (1996). Phylogenetic Perspectives on Community Ecology. *Ecology*, 77, 1344–1354.
- 470 Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship  
471 between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.*, 11, 995–  
472 1003.
- 473 Losos, J.B. (2011). Seeing the Forest for the Trees: The Limitations of Phylogenies in  
474 Comparative Biology. *Am. Nat.*, 177, 709–727.
- 475 Martins, E.P. & Hansen, T.F. (1997). Phylogenies and the Comparative Method: A General  
476 Approach to Incorporating Phylogenetic Information into the Analysis of Interspecific Data. *Am.*  
477 *Nat.*, 149, 646–667.
- 478 McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology  
479 from functional traits. *Trends Ecol. Evol.*, 21, 178–185.
- 480 Moen, D.S., Smith, S.A. & Wiens, J.J. (2009). Community Assembly Through Evolutionary  
481 Diversification and Dispersal in Middle American Treefrogs. *Evolution*, 63, 3228–3247.
- 482 Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B. & Westoby, M. (2005). A  
483 Brief History of Seed Size. *Science* (80- ), 307, 576–580.
- 484 Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884.
- 485 Pearse, W.D., Cadotte, M.W., Cavender-Bares, J., Ives, A.R., Tucker, C.M. & Walker, S.C. *et al.*  
486 (2015). Pez: Phylogenetics for the environmental sciences. *Bioinformatics*, 31, 2888–2890.
- 487 Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H. & Jaureguiberry, P. *et al.*  
488 (2013). New handbook for standardised measurement of plant functional traits worldwide. *Aust.*  
489 *J. Bot.*, 61, 167–234.
- 490 Pollock, L.J., Morris, W.K. & Vesik, P.A. (2012). The role of functional traits in species  
491 distributions revealed through a hierarchical model. *Ecography*, 35, 716–725.

- 492 R Core Team. (2015). R: A Language and Environment for Statistical Computing.
- 493 Ricklefs, R.E. & Schluter, D. (1993). Species diversity in ecological communities: Historical and  
494 geographical perspectives. In: *Species diversity in ecological communities: Historical and*  
495 *geographical perspectives*. University of Chicago Press.
- 496 Self, S.G. & Liang, K.-Y. (1987). Asymptotic Properties of Maximum Likelihood Estimators  
497 and Likelihood Ratio Tests Under Nonstandard Conditions. *J. Am. Stat. Assoc.*, 82, 605–610.
- 498 Stamatakis, A. (2014). RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis  
499 of Large Phylogenies. *Bioinformatics*, btu033.
- 500 Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991). What to protect? Systematics and  
501 the agony of choice. *Biol. Conserv.*, 55, 235–254.
- 502 Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C. & Hummel, I.*et al.* (2007). Let the  
503 concept of trait be functional! *Oikos*, 116, 882–892.
- 504 Warton, D.I., Foster, S.D., Death, G., Stoklosa, J. & Dunstan, P.K. (2014). Model-based thinking  
505 for community ecology. *Plant Ecol.*, 1–14.
- 506 Webb, C.O. (2000). Exploring the phylogenetic structure of ecological communities: An  
507 example for rain forest trees. *Am. Nat.*, 156, 145–155.
- 508 Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008). Phylocom: Software for the analysis of  
509 phylogenetic community structure and trait evolution. *Bioinformatics*, 24, 2098–2100.
- 510 Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002). Phylogenies and  
511 community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475–505.
- 512 Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil*, 199,  
513 213–227.
- 514 Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B. & Cornell, H.V.*et al.*  
515 (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol.*  
516 *Lett.*, 13, 1310–1324.

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521 **Tables:**

522

523 **Table 1** Estimated variance of random effects for the PLMM (equation 1) used to detect phylogenetic  
 524 patterns in community composition.

PLMM	$\sigma_a^2$	$\sigma_b^2$	$\sigma_c^2$	$\sigma_d^2$	$\sigma_e^2$	$p(\sigma_c^2 = 0)$	AIC
Phylogenetic attraction:							
$c \sim \text{Gaussian}(\mathbf{0}, \text{kron}(\mathbf{I}_m, \sigma_c^2 \mathbf{\Sigma}_{\text{spp}}))$	0.98	0	$6.50 \times 10^{-3}$	0	0.5154	0.008	3900
Phylogenetic repulsion:							
$c \sim \text{Gaussian}(\mathbf{0}, \text{kron}(\mathbf{I}_m, \sigma_c^2 (\mathbf{\Sigma}_{\text{spp}})^{-1}))$	0.98	0	0	$2.28 \times 10^{-2}$	0.5308	0.496	3906
Non-nested model:							
$c$ removed	0.98	$2.29 \times 10^{-2}$	-	0	0.5306	-	3904

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526

527 **Table 2** Phylogenetic signal and site variation for each functional trait. P-values for the null hypothesis  $\sigma_b^2$   
 528 = 0 (equation 2) implying no difference among sites in the effects of trait values on log abundance are  
 529 given in the column labeled  $p(\sigma_b^2 = 0)$ . Functional traits with strong phylogenetic signal and  $p(\sigma_b^2 = 0) <$   
 530 0.1 are considered to be important in explaining phylogenetic patterns.

Trait	Pagel's $\lambda$	$K$	$p(\sigma_b^2 = 0)$
<b>Leaf specific area (SLA, <math>m^2/kg</math>)</b>	0.70**	0.26**	<b>0.002</b>
<b>Leaf circularity (Dimensionless)</b>	1.00***	0.71***	<b>0.001</b>
<b>Leaf thickness (<math>mm</math>)</b>	0.96***	1.80***	<b>0.001</b>
<b>Leaf width (<math>cm</math>)</b>	0.98***	0.56***	<b>0.008</b>
<b>§Animal dispersal (Yes or no)</b>	0.65***	0.28**	<b>0.054</b>
Life cycle (Annual or non-annual)	0.00	0.30	0.479
Growth habit (woody or non-woody)	1.08***	0.24**	0.500
Pollination mode (Biotic or abiotic)	0.00	0.08	0.500
Seed mass ( $g/seed$ )	0.56	0.30	0.373
Leaf dry mass content (LDMC, %)	0.51	0.16	0.500
Stem dry mass content (SDMC, %)	0.00	0.14	0.500
Plant height ( $cm$ )	0.71**	0.17**	0.500
Leaf length ( $cm$ )	0.96***	0.32**	0.500
Leaf carbon content (%)	0.65**	0.26**	0.500
Leaf nitrogen content (%)	0.34	0.09	0.334
Wind dispersal (Yes or no)	1.17***	0.46***	0.265
Unassisted dispersal (Yes or no)	0.00	0.15	0.500

531 \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

532

533 **Table 3** Reduction of the phylogenetic variance in community composition caused by the inclusion of  
534 functional traits (equation 3).

Trait	$\sigma_c^2$ with traits	$\sigma_c^2$ without traits	$100 \times \sigma_c^2(\text{with traits}) / \sigma_c^2(\text{without traits})$
Leaf width	0.005302	0.006457	17.89
Leaf thickness	0.005921	0.006457	8.30
SLA	0.006024	0.006457	6.71
Leaf circularity	0.006310	0.006457	2.28
Animal dispersal	0.006380	0.006456	1.18
SLA + circularity + thickness + Leaf width + Animal dispersal	0.002804	0.006480	56.73

535

536

537 **Table 4** Variation in the response of species abundances to environmental variables (equation 4).  
 538 Although 13/20 environmental variables generated variation in species composition among communities,  
 539 none of these showed phylogenetic signal in which related species responded more similarly to the  
 540 environmental variable.  
 541

Environmental variables	<i>P</i> -values $\sigma_g^2$ (no phylogenetic signal)	<i>P</i> -values for $\sigma_h^2$ (phylogenetic signal)
Minimum temperature	< <b>0.001</b>	0.500
Precipitation	< <b>0.001</b>	0.500
Canopy shade	<b>0.002</b>	0.500
Total exchange capacity	<b>0.002</b>	0.500
Organic matter	<b>0.001</b>	0.500
pH	< <b>0.001</b>	0.500
N	< <b>0.001</b>	0.500
P	<b>0.039</b>	0.500
Mg	<b>0.030</b>	0.500
K	<b>0.007</b>	0.500
Na	< <b>0.001</b>	0.500
Mn	< <b>0.001</b>	0.354
Ca	< <b>0.001</b>	0.122
Clay	0.110	-
Silt	0.070	-
Sand	0.117	-
Fe	0.500	-
S	0.458	-
Zn	0.500	-
Al	0.500	-

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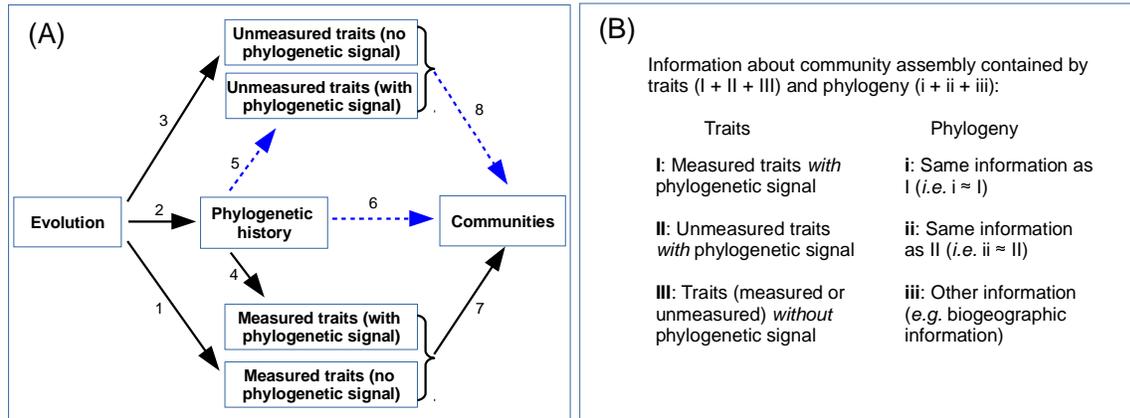
543 **Figures:**

544 **Figure 1** Schematic diagram of the conceptual framework of the study. (A) Evolution is the  
545 ultimate source of all trait values, although only some traits have phylogenetic signal that reflects  
546 phylogenetic history (arrows 2, 4 and 5). Other traits do not (arrows 1 and 3), possibly because  
547 these traits evolve rapidly or experience convergent evolution. Community composition is  
548 determined by unmeasured and measured traits, and also by additional processes that could  
549 generate phylogenetic signal, such as biogeographical patterns in the distribution of species.  
550 Phylogenetic patterns in community composition can be generated from measured and  
551 unmeasured traits with phylogenetic signal (arrows 7 and 8), and by other phylogenetic processes  
552 (arrow 6). The question we address is how much of the phylogenetic signal in community  
553 composition can be explained by measured functional traits, and whether after accounting for  
554 these traits there is residual phylogenetic signal that could have been generated by unmeasured  
555 traits or other phylogenetic processes. (B) Traits and phylogeny contain overlapping and  
556 complementary information about how communities are assembled. Here, we focus on  
557 estimating the proportion of this overlapping information that the phylogeny contains (i.e., the  
558 magnitude of  $i$  relative to  $i + ii + iii$ ). Note that we do not try to explain the proportion of  
559 overlapping information that functional traits contain (i.e., the magnitude of  $I$  relative to  $I + II +$   
560  $III$ ) due to our inability to estimate the amount of information provided by unmeasured traits and  
561 hence estimate  $(I + II + III)$ .

562 **Figure 2:** Phylogeny and relative abundance of the 55 common plant species found in the pine  
563 barrens of central Wisconsin in 2012. The area of dots is proportional to abundances within each  
564 site.

565

566

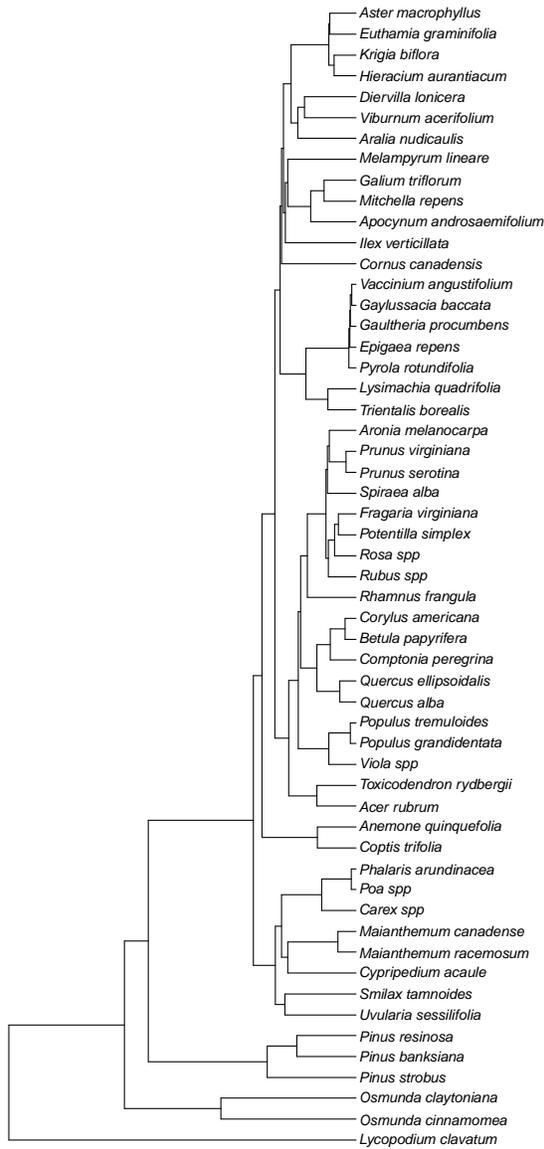


567

568

Figure 1

Sites



569

570 Figure 2

571

## 572 Appendix

573 In the Appendix we give Tables S1-S4 that correspond to Tables 1-4 in the main text, but using a  
 574 PGLMM for presence/absence data. The equations used for the PGLMM are the same as equations 1-4,  
 575 but for binomial data; for example, the PGLMM corresponding to equation 1 is  
 576  $\Pr(Y_i = 1) = \text{logit}^{-1}(a + a_{\text{spp}[i]} + b_{\text{spp}[i]} + c_i + d_{\text{site}[i]}),$   
 577 with other terms identical.

578

579

580 **Table S1** Estimated variance of random effects within the phylogenetic generalized linear mixed model  
 581 used to detect phylogenetic patterns comparable to equation 1, where phylogenetic attraction and  
 582 phylogenetic repulsion are estimated by  $\sigma_c^2$ .

583

PGLMM	$\sigma_a^2$	$\sigma_b^2$	$\sigma_c^2$	$\sigma_d^2$	$p(\sigma_c^2 = 0)$
Phylogenetic attraction:					
$c \sim \text{Gaussian}(\mathbf{0}, \text{kron}(\mathbf{I}_m, \sigma_c^2 \boldsymbol{\Sigma}_{\text{spp}}))$	2.84	0	0.0452	0.01	<0.001
Phylogenetic repulsion:					
$c \sim \text{Gaussian}(\mathbf{0}, \text{kron}(\mathbf{I}_m, \sigma_c^2 (\boldsymbol{\Sigma}_{\text{spp}})^{-1}))$	3.10	0	0.0011	0.19	0.5
Non-nested model: $c$ removed	2.83	0	-	0.18	-

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602 **Table S3** Proportion of phylogenetic signal of species composition in communities explained by  
603 individual functional trait and multiple functional traits. With selected multiple functional traits, about  
604 61% percent of phylogenetic variation was explained, suggesting that phylogenies can provide additional  
605 information about community assembly beyond measured functional traits. See equation 3 in the Methods  
606 section for details about models.  
607

Trait	$\sigma_c^2$ with trait	$\sigma_c^2$ without trait	$100 \times \sigma_c^2(\text{with trait}) / \sigma_c^2(\text{without trait})$
Leaf width	0.018105	0.041847	56.74
Leaf thickness	0.030925	0.041847	26.10
Leaf circularity	0.035442	0.041854	15.32
SLA	0.036811	0.041828	12.00
Wind dispersal	0.039946	0.041844	4.54
Animal dispersal	0.041534	0.041862	0.78
Leaf width + Leaf thickness + Leaf circularity + SLA + Wind dispersal + Animal dispersal	0.004616	0.041834	88.97

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619 **Table S4** There are strong variations in species' relationships between their presence/absence and most  
 620 environmental variables (*p* value of each environmental variable was presented in the *P*-values for  
 621 variation column). Four of these variations show phylogenetic signal. For environmental variable that has  
 622 no strong variation in species' responses, no further test for phylogenetic signal of variation was  
 623 conducted (thus "-" in the third column). P-values that are less than 0.05 are in bold.  
 624

Environmental variables	P-values for variation	P-values for phylogenetic signal of variation
<b>Minimum temperature</b>	<b>&lt;0.001</b>	<b>0.002</b>
Precipitation	<b>&lt;0.001</b>	0.500
Canopy shade	<b>0.001</b>	0.500
Total exchange capacity	0.149	-
Organic matter	0.161	-
<b>pH</b>	<b>0.005</b>	<b>&lt;0.001</b>
N	0.052	-
P	0.343	-
Mg	0.500	-
K	0.206	-
Na	<b>0.004</b>	0.500
<b>Mn</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
<b>Ca</b>	<b>0.012</b>	<b>&lt;0.001</b>
Clay	0.431	-
Silt	0.494	-
Sand	0.500	-
Fe	0.379	-
S	0.500	-
Zn	0.500	-
Al	0.500	-

625

626 Text S1 Code to compare  $p$ -values of null hypothesis  $\sigma^2 = 0$  calculated from the  $0.5\chi_0^2 + 0.5\chi_1^2$   
627 mixture distribution and parametric bootstrap. The  $p$ -values based on the mixture Chi-square  
628 distribution are conservative (i.e. higher than those from parametric bootstrap).

```
629 # packages used
630 library(ape) # for phylogeny reading
631 library(plyr)
632 library(MASS)
633 library(dplyr, quietly = TRUE)
634 library(pez) # for communityPGLMM function
635 library(parallel) # for multiple cores parallel computation, not available
636 # for Windows operation system

637 # data: vegetation data, phylogeny
638 load("d_li_data.RData")
639 # select 20 sites and 20 species of veg data in 1958 as an example
640 test = veg.aggr.wide.1958[1:20, 1:20]
641 test1 = filter(veg.aggr.long.1958, sp %in% names(test), site %in% rownames(test))
642
643
644 # this function calculates log likelihood of the fitted model on observed
645 # data, then simulates data based on the fitted model, and fits model on
646 # simulated data and calculates the log likelihood of the fitted model; then
647 # calculates the p-value of the log likelihood of the fitted model on
648 # observed data based all simulated ones (i.e. parametric bootstrap); so we
649 # can compare the p-value get in this way (parametric bootstrap) with the
650 # one from the mixture Chi-square distribution.
651 q1_obs_sim = function(veg.long, phylo = pb.phylo, date = 1958, trans = NULL,
652   nsim = 100, ncores = 5) {
653   # transformation of freq
654   if (!is.null(trans)) {
655     if (trans == "log") {
656       veg.long$Y <- log(veg.long$freq + 1)
657     }
658
659     if (trans == "asin") {
660       veg.long <- group_by(veg.long, site) %>% mutate(Y = asin(sqrt((freq + 1)/ifelse(date == 1958, 20 + 2, 50 + 2)))) %>% ungroup() %>%
661         as.data.frame()
662     }
663   }
664
665   veg.long$sp = as.factor(veg.long$sp)
666   veg.long$site = as.factor(veg.long$site)
667   nspp <- nlevels(veg.long$sp)
668   nsite <- nlevels(veg.long$site)
669
670
671   # Var-cov matrix for phylogeny
672   phy <- drop.tip(phylo, tip = phylo$tip.label[!phylo$tip.label %in% levels
673     (veg.long$sp)])
```

```
674 Vphy <- vcv(phy)
675 Vphy <- Vphy[order(phy$tip.label), order(phy$tip.label)]
676 Vphy <- Vphy/max(Vphy)
677 Vphy <- Vphy/det(Vphy)^(1/nspp)
678 Vphy.inv = solve(Vphy)
679
680 show(c(nlevels(veg.long$sp), Ntip(phy))) # should be equal
681
682 # random effect for site
683 re.site <- list(1, site = veg.long$site, covar = diag(nsites))
684 re.sp <- list(1, sp = veg.long$sp, covar = diag(nspp))
685 re.sp.phy <- list(1, sp = veg.long$sp, covar = Vphy)
686 # sp is nested within site, to test phylo attraction or repulsion
687 re.nested.phy <- list(1, sp = veg.long$sp, covar = Vphy, site = veg.long$
688 site)
689 re.nested.rep <- list(1, sp = veg.long$sp, covar = Vphy.inv, site = veg.l
690 ong$site)
691
692 z <- communityPGLMM(Y ~ 1, data = veg.long, family = "gaussian", sp = veg
693 .long$sp, site = veg.long$site, random.effects = list(re.sp, re.sp.phy, re.si
694 te, re.nested.phy), REML = F, verbose = F, s2.init = 0.1)
695 show(z$ss)
696 z0 <- communityPGLMM(Y ~ 1, data = veg.long, family = "gaussian", sp = ve
697 g.long$sp, site = veg.long$site, random.effects = list(re.sp, re.sp.phy, re.s
698 ite),
699 REML = F, verbose = F, s2.init = 0.1)
700 z.rep <- communityPGLMM(Y ~ 1, data = veg.long, family = "gaussian", sp =
701 veg.long$sp, site = veg.long$site, random.effects = list(re.sp, re.sp.phy, r
702 e.site, re.nested.rep), REML = F, verbose = F, s2.init = 0.1)
703 show(z.rep$ss)
704
705 # observed output, p-values are get from Chisq approx.
706 output_obs = data.frame(LRT_attract = (z$logLik - z0$logLik), p_attract =
707 pchisq(2 * (z$logLik - z0$logLik), df = 1, lower.tail = F)/2, LRT_repulse =
708 (z.rep$logLik - z0$logLik), p_repulse = pchisq(2 * (z.rep$logLik - z0$logLik)
709 , df = 1, lower.tail = F)/2, obs_sim = "obs")
710
711 # the fitting model z0:  $\log(y_i + 1) = \alpha + a_{spp}[i] +$ 
712 #  $b_{spp.phy}[i] + c_{site}[i] + err[i]$ 
713
714 alpha = z0$B # intercept, overall mean of all sp
715 alpha.se = z0$B.se # SE
716 LRT_sim = mclapply(1:nsim, function(x) {
717 # multi-cores
718 set.seed(x)
719 # z0$ss: random effects' SD for the cov matrix  $\sigma^2 * V$ , in order
720 : [1]
721 # sp with no phylo; [2] sp with Vphy; [3] site random effect
722 a_spp = rnorm(nspp, 0, z0$ss[1]) # simulate a_spp
```

```
722     # simulate b_spp.phy
723     b_spp.phy = MASS::mvrnorm(1, mu = rep(0, nspp), Sigma = z0$ss[2] * Vp
hy)
724
725     mu_spp = alpha + a_spp + b_spp.phy # mean freq of sp
726     c_site = rnorm(nsite, 0, z0$ss[3]) # site random
727     mu_spp_site = rep(mu_spp, nsite) + rep(c_site, each = nspp) # each s
728     p at each site
729     y_i = rnorm(nspp * nsite, mean = mu_spp_site, sd = alpha.se) # inclu
730     de SE of intercept
731     y_i_count = ceiling(exp(y_i) - 1) # exp transf and round to positive
732     interge
733     test1_sim = data.frame(sp = names(mu_spp_site), site = rep(1:nsite,
734     each = nspp), Y = y_i, freq = y_i_count)
735
736     test1_sim$sp = as.factor(test1_sim$sp)
737     test1_sim$site = as.factor(test1_sim$site)
738
739     # refit models on simulated data random effect for site
740     re.site.sim <- list(1, site = test1_sim$site, covar = diag(nsite))
741     re.sp.sim <- list(1, sp = test1_sim$sp, covar = diag(nspp))
742     re.sp.phy.sim <- list(1, sp = test1_sim$sp, covar = Vphy)
743     # sp is nested within site
744     re.nested.phy.sim <- list(1, sp = test1_sim$sp, covar = Vphy, site =
745     test1_sim$site)
746     re.nested.rep.sim <- list(1, sp = test1_sim$sp, covar = Vphy.inv, sit
747     e = test1_sim$site)
748
749     z_sim <- communityPGLMM(Y ~ 1, data = test1_sim, family = "gaussian",
750
751     sp = test1_sim$sp, site = test1_sim$site, random.effects = list(r
752     e.sp.sim, re.sp.phy.sim, re.site.sim, re.nested.phy.sim), REML = F, verbose =
753     F, s2.init = 0.1)
754     # show(z_sim$ss)
755     z0_sim <- communityPGLMM(Y ~ 1, data = test1_sim, family = "gaussian"
756     , sp = test1_sim$sp, site = test1_sim$site, random.effects = list(re.sp.sim,
757     re.sp.phy.sim, re.site.sim), REML = F, verbose = F, s2.init =
758     0.1)
759
760     # show(z0_sim$ss)
761     z.rep_sim <- communityPGLMM(Y ~ 1, data = test1_sim, family = "gaussi
762     an", sp = test1_sim$sp, site = test1_sim$site, random.effects = list(re.sp.si
763     m, re.sp.phy.sim, re.site.sim, re.nested.rep.sim), REML = F, verbose = F, s2.
764     init = 0.1)
765     # show(z.rep_sim$ss)
766
767     # Log lik of refitted models on simulated data
768     data.frame(LRT_attract = (z_sim$logLik - z0_sim$logLik), LRT_repulse
769     = (z.rep_sim$logLik - z0_sim$logLik))
    }, mc.cores = ncores)
```

```
770
771
772     # output results
773     list(output_obs, ldply(LRT_sim))
774 }
775
776 qqq = q1_obs_sim(test1, trans = "log", nsim = 1000, ncores = 6)
777 saveRDS(qqq, "qqq.rds")
778
779 qqq = readRDS("qqq.rds")
800 qqq[[1]]
801
802 ##   LRT_attract p_attract  LRT_repulse p_repulse obs_sim
803 ## 1  0.3006013 0.2190598 -1.82719e-05      0.5      obs
804
805 head(qqq[[2]])
806
807 ##   LRT_attract  LRT_repulse
808 ## 1  -0.9611412 -15.68606765
809 ## 2   0.1303866  -0.14712624
810 ## 3  -2.9661583   0.06437319
811 ## 4  -0.2152182  -1.91538503
812 ## 5  -0.4204626   0.04073069
813 ## 6  -1.3125998  -0.40523844
814
815 qqq[[2]]$obs_sim = "sim"
816 q1_sim = rbind(select(qqq[[1]], -p_attract, -p_repulse), qqq[[2]])
817 1 - (rank(q1_sim$LRT_attract)[1] + 1)/1001 # 0.12088 vs 0.219 from Chisq
818
819 ## [1] 0.1208791
820
821 1 - (rank(q1_sim$LRT_repulse)[1] + 1)/1001 # 0.40959 vs 0.5 from Chisq
822
823 ## [1] 0.4095904
```